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A COMPARISON OF THE SEED BANKS OF SAND DUNES WITH DIFFERENT DISTURBANCE HISTORIES ON CAPE COD NATIONAL SEASHORE

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ABSTRACT. The seed bank compositions of four different coastal sand dunes on Cape Cod National Seashore (Massachusetts, USA) were characterized and used to predict the potential of seed banks in restoring species diversity in degraded sand dunes. Seedling emergence from sand collected from each site was observed over 15 weeks. A total of 254 seedlings emerged during the study. A single species, *Artemisia caudata*, was responsible for 85% of the total seedling emergence, and all but one of those seedlings was from a single study site. Overall, seedling emergence and the species diversity of seedlings was low, indicating a low density of seeds in the sand dune substrate. Seedlings emerged from only 20% of the sand samples, indicating that the distribution of seeds in the sand is tightly clustered. The lowest numbers of seedlings emerged from the most severely degraded site which had recently been replanted with *Ammophila breviligulata* (American Beachgrass). Potential reasons for this clumping of seedlings are discussed, including poor seed dispersal as a result of buried mature infructescences or as a result of wind deposition of seeds in small depressions. The results suggest that the existing seed bank is unlikely to lead to significant increases in species diversity at sites undergoing restoration. Consequently, the importation of sand and its associated seed bank from more mature sites is not a feasible means of restoring diversity because of the low density and species diversity of seeds in the sand at more stable sites.

Key Words: Cape Cod National Seashore, disturbance history, sand dune ecology, seed bank

Soil seed banks play important roles in plant community dynamics. Buried seeds provide a source of new recruits into plant populations and can greatly influence the species composition and density of individuals in a community, especially following a disturbance event. Some species may persist in the seed bank in a dormant, but viable, state for hundreds of years before proper conditions for germination and emergence return them to the adult community (Baker 1989). During the dormancy period, substantial changes in the community composition may have oc-

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curred. Previous studies have found that the composition and abundance of species in the soil seed bank do not necessarily reflect the composition and abundance of aboveground adults in the same area (Major and Pyott 1966; Thompson and Grime 1979; Whipple 1978). However, frequently disturbed areas often show a close correlation between adult vegetation and the soil seed bank (Henderson et al. 1988). In addition to their ecological and evolutionary significance (reviewed in Fenner 1985, 1992; Leck et al. 1989), soil seed banks may also have important implications for habitat conservation and management (Keddy et al. 1989). Soil seed banks have been used successfully in restoration of abandoned surface coal mines (Johnson and Bradshaw 1978). Van der Valk and Pederson (1989) have reviewed the use of seed banks in habitat restoration and suggest that soil seed banks have great potential for the restoration of degraded habitat.

The plant communities of Cape Cod, Massachusetts, have experienced severe anthropogenic disturbance since European colonization of New England and much effort has been devoted to their restoration. Extensive logging and grazing resulted in almost complete deforestation of the outer Cape (Eastham, Wellfleet, Truro, Provincetown) by the early 1800s (Westgate 1904). Removal of the vegetation caused extensive sand erosion. Fierce winter winds, rain, and snow began moving and shaping the bare sand dunes that still exist today. Sand control efforts in the Province Lands of the outer Cape began in 1825 when the moving sand not only buried homes but also threatened Provincetown's greatest economic asset, the harbor (Hawk and Sharp 1967; Westgate 1904). American Beachgrass, *Ammophila breviligulata*, was found to be the only plant that could survive in the moving sand and effectively stabilize it. Although large expanses of planted *A. breviligulata* to some extent have now stabilized sand dunes, these replantings have not re-created the biodiversity of undisturbed dunes which support a greater diversity of species. Stabilized areas that receive gradual sand accumulations may be colonized by annuals such as *Cakile edentula* and *Xanthium echinatum* Murr. and herbaceous perennials such as *A. breviligulata*, *Solidago sempervirens*, *Artemisia caudata*, and *Lathyrus japonicus* (Stalter 1993). Shrubs such as *Hudsonia tomentosa*, *Arctostaphylos uva-ursi* (L.) Spreng., *Myrica pensylvanica*, *Rosa rugosa*, and *Prunus maritima*, and finally, trees such as *Pinus rigida*

Miller and *Quercus* spp. may invade and eventually dominate the areas.

In 1963 the Cape Cod National Seashore (CCNS) took over the role of sand control on most of the outer Cape. Extensive efforts have been undertaken to restore the degraded coastal sand dune ecosystems within the boundaries of the CCNS. *Ammophila breviligulata*, a clonal perennial grass with spreading rhizomes, has been planted extensively with the primary goal of stabilizing the moving sand. Other methods have been examined such as the addition of inorganic fertilizer and inoculation of the soil with mycorrhizal fungi (Koske and Gemma 1992) in order to improve the vigor of *A. breviligulata* plantings. The potential for existing seed banks to promote natural succession and revegetation of the sand dunes has not been examined, however. We propose that sand dunes that have been disturbed and replanted with *A. breviligulata* have a lower species richness and buried seed density than those dunes that have experienced less human disturbance. In this study, we examine the composition and abundance of species in the seed bank of four sand dunes on Cape Cod National Seashore with different past disturbance and recovery histories. Due to the unique disturbance history and recovery of each site, each site is evaluated individually and then compared with each other site. The data will be used to predict the potential for the seed banks at replanted sites to increase species diversity in the future, and the potential for seed banks from undisturbed sites to be used in restoring degraded sites.

MATERIALS AND METHODS

Field sites. All study sites were located in backdune areas dominated by *Ammophila breviligulata* within the boundaries of Cape Cod National Seashore, Massachusetts, USA. The study sites consisted of two areas that had been replanted with *A. breviligulata* following severe anthropogenic disturbance and two areas that had received little human disturbance and had never been replanted.

The High Head site (42°15′N, 70°10′W) is located east of Pilgrim Lake in the town of Truro. Severe anthropogenic disturbance has destroyed much of the vegetation on the sand dunes adjacent to Pilgrim Lake. Unlike all the other sites, which are adjacent to beaches, this site is in a depression behind parabolic secondary dunes that are moving in a southeasterly direction at a rate of 10–20 ft. per year toward Pilgrim Lake (Madore and Leatherman 1981). The sampling site gradually rises up from the bottom of the depression at a 10–20% grade. In an effort to stabilize the moving sand, the area was planted with rows of nursery-raised *Ammophila breviligulata* in 1989 (Koske and Gemma 1992).

The Marconi Station site is due east of the water tower near the CCNS headquarters in South Wellfleet, between Marconi Beach and the Guglielmo Marconi Memorial (41°55′N, 69°59′W). This area was subject to heavy military activity until 1963 when CCNS was established and was subsequently bulldozed and replanted with *Ammophila breviligulata* and allowed to revegetate naturally over the past three decades (David Crary, National Park Service, Fire Management Officer, pers. comm.). A three-year study has recorded negligible sand movement at this relatively flat site (Shumway, unpubl. data). A rapidly and severely eroding 20 m high cliff separates the beach from the study site, possibly reducing the deposition of new sand characteristic of many backdunes.

The Coast Guard Beach site is located south of the Coast Guard Environmental Education Center between Nauset Marsh and Coast Guard Beach in Eastham (41°45′N, 69°55′W). This barrier beach system, which experiences stochastic overwash events, is situated between an ocean beach and a salt marsh that is flooded by an inlet located further south. Because of rising sea levels and oceanic storms, this relatively flat area is undergoing "retreat," pushing the Coast Guard barrier beach westward onto the salt marsh (Godfrey 1979). An aerial photo taken on 12 September 1970 (CCNS aerial photo #8207, D. Crary, pers. comm.) shows that the location of the sampling site was actually part of the salt marsh at that time. The site experienced a number of anthropogenic disturbances until 1978 when the parking lot located adjacent to the site was destroyed by a winter storm. Since then, CCNS has curtailed foot traffic to prevent further erosion and protect nesting shore birds. This site represents a young dune system that has been vegetated naturally and thus will be considered a control in this study.

The Duck Harbor site (41°57′N, 70°04′W) is located north of Great Island in Wellfleet. The site, located between the beach overlooking Cape Cod Bay and a freshwater spring, occupies a total width of approximately 150 m. Because the primary dune separating the beach and the backdune area is only about 3 to 5 m high, this site has a gradual incline of 10–20% and is likely to receive considerable sand deposition (T. Baptista, pers. obs.). Aerial photos of Duck Harbor from 1938, 1960, 1974, and 1987 do not show any significant differences in the shape and extension of the dunes (CCNS library collection). Hand-drawn maps from 1856 (CCNS library) show that Duck Harbor beach was open to the ocean and connected to a small river system that extended inland. Sand deposition closed off the harbor about 120 years ago. An off-road vehicle trail through the site was closed about ten years ago and the site presently receives moderate foot traffic (D. Crary, pers. comm.). There is no evidence that the area has ever been replanted.

Seed bank characterization. Seed bank composition was determined for each site by observing seedling emergence from field-collected substrate samples. Direct determination of the seed bank composition was also attempted by sifting substrate samples with sieves of decreasing mesh sizes followed by suspending the organic matter in saline solutions. These methods proved ineffective because of poor and variable recovery rates (data not included) and will not be discussed further. See Roberts (1981) and Gross (1990) for discussions of standard methods for seed bank determinations.

Substrate samples from High Head, Duck Harbor, and the Marconi Station were collected on 13 March 1994 and from Coast Guard Beach on 20 March 1994. Substrate samples were collected in late winter after buried seeds had been exposed to a natural cold stratification period. Previous studies have found that soils exposed to seasonal chilling yield more seedlings than samples collected before winter (Leck and Graveline 1979; Raynal and Bazzaz 1973).

Samples were removed from a cylindrical core with a depth of 10 cm and diameter of 15 cm for a total volume of 1767 cm^3. At each site, one sample was collected every 10 m along each of four 100 m long parallel transects (10 m apart) using a stratified sampling method (Hutchings 1991) for a total of 40 samples per site.

In the germination experiment, 38 substrate samples from each site (because of greenhouse space constraints two random samples from each site were discarded) were each spread out in 25 cm × 25 cm × 6 cm plastic trays containing a 3 cm deep layer of potting soil for a total depth of 5 cm. The addition of the potting soil layer (Peters Professional "Redi Earth" potting soil and seed starting mix) increased the sample volume and helped to slow the rate of dessication of the thinly spread samples. Replicates were misted daily with tap water. Room temperature was maintained at 25–30°C. Banks of forty-watt wide-spectrum grow-lights positioned 15 cm above the samples provided a photoperiod of 16 hr. of light per day. The trays were examined for newly emerging seedlings at weekly intervals for 15 weeks. Upon identification the seedlings were removed from the trays. Trays were randomized on the greenhouse bench after each census in order to account for possible variations in ambient conditions (e.g., temperature, light intensity, etc.).

Adult vegetation survey. In order to compare aboveground vegetation with the seed bank at each site, adult species composition and density were determined along the same transects at each site on 22 May 1994. A 0.50 × 0.50 m quadrat was placed every ten meters and stem density (stems/0.25 m^2) was recorded for each species present. In order to more fully measure species richness we also recorded the identity and estimated the relative abundance (Dominant > Abundant > Frequent > Occasional > Rare; Mueller-Dombois and Ellenberg 1974) of all species that were observed growing at each site.

RESULTS

Seed bank characterization. A total of 254 seedlings emerged over the 15-week experiment in only 20% of the 152 samples (see frequencies in Table 1), indicating a highly clumped distribution of seeds in the sand. Eighty-nine percent of the seedlings originated from the Duck Harbor site. The Marconi Station and Coast Guard Beach sites were each responsible for 5%, and the High Head site contributed only 0.8%, of the total seedling emergence (Table 1). There was a statistically significant difference in the total number of seedlings emerging across the sites ($\chi^2 = 709.76$, $p < 0.001$).

The most common species in the seedling emergence experiment (85%) was *Artemisia caudata*. Of the 217 *A. caudata* seedlings that emerged, all but one originated from Duck Harbor sam-

Table 1. Results of the seed bank characterization experiment for each study site (N = 38). Top value = total number of seedlings emerging across all replicates. Middle value = mean (±SD) number of seedlings emerging per replicate. Bottom value = the frequency of seedling emergence in replicates (number of replicates in which seedlings emerged/total number of replicates × 100%). *p < 0.05, chi-square test comparing seedling emergence across study sites.

Species		High Head	Marconi Station	Coast Guard Beach	Duck Harbor
Ammophila breviligulata	*	1	6	6	0
		0.03 ± 0.16	0.16 ± 0.82	0.16 ± 0.68	0
		3	5	5	0
Artemisia caudata	*	0	0	1	216
		0	0	0.03 ± 0.16	5.7 ± 19.4
		0	0	3	29
Chenopodium rubrum		0	1	2	1
		0	0.03 ± 0.16	0.05 ± 0.23	0.03 ± 0.16
		0	3	5	3
Hudsonia spp.		0	2	0	0
		0	0.05 ± 0.23	0	0
		0	5	0	0
Solidago sempervirens		0	3	1	4
		0	0.08 ± 0.27	0.03 ± 0.16	0.10 ± 0.50
		0	8	3	5
Other species		1	1	2	6
		0.03 ± 0.16	0.03 ± 0.16	0.05 ± 0.23	0.15 ± 0.43
		3	3	5	13
Total	*	2	13	12	227
		0.05 ± 0.23	0.34 ± 1.07	0.32 ± 0.84	5.97 ± 19.8
		5	16	18	44

ples. Eighty-seven percent of the *A. caudata* seedlings emerged from three replicates and the remainder from eight other replicates. When *A. caudata* was removed from the data, differences in seedling emergence among the four sites still remained statistically significant ($\chi^2 = 8.11$, $p < 0.05$). The second most common seedling species, *Ammophila breviligulata*, emerged in the High Head, Marconi Station, and Coast Guard Beach samples, making up 5% of the total number of seedlings.

Solidago sempervirens, which made up 3% of all seedlings, emerged at all the sites except High Head. All together, the *Chenopodium rubrum* L., *Hudsonia* spp., *Artemisia stelleriana*, *Cakile edentula*, and *Polygonella articulata* seedlings made up less than 2% of all seedlings (the latter three species are listed under the "Other Species" category in Table 1).

Adult vegetation survey. *Ammophila breviligulata* was clearly the numerically dominant adult species at all four sites; however, it differed in abundance between sites (Table 2). The lowest *A. breviligulata* stem densities were found at the replanted sites with 10.2 ± 3.7 and 12.6 ± 5.8 (X ± S.D.) stems/0.25 m^2 at High Head and the Marconi Station, respectively. Duck Harbor averaged 23.1 ± 11.0 stems/0.25 m^2 and Coast Guard had the highest density of 37.4 ± 14.2 stems/0.25 m^2. *Ammophila breviligulata* was the only species to occur in 100% of the quadrats at all four sites. *Solidago sempervirens* was the second most abundant species at Marconi Station and Duck Harbor, yet averaged less than 3.2 individuals/0.25 m^2 and had a frequency of occurrence of less than 67%. Each of the other species averaged fewer than 1.9 individuals/0.25 m^2 and appeared in quadrats with a frequency of less than 46% (Table 2).

Marconi Station, Duck Harbor, and Coast Guard Beach had similar adult species richness with 9, 11, and 12 species, respectively (Table 3). *Ammophila breviligulata* and *Solidago sempervirens* were consistently the most abundant species at these sites. In marked contrast, High Head supported only *A. breviligulata* and the annual *Polygonella articulata*.

DISCUSSION

The seed banks at all four sand dune study sites are characterized by low species richness, low densities of viable seeds, and highly clumped distributions of seeds within the soil. The average

Table 2. Results of the adult vegetation survey for each study site (N = 40). Top value = the mean density (±SD) of adults/0.25 m^2 at each site. Bottom value = the frequency of occurrence of each species (number of quadrats containing the species/40 × 100%).

Species	High Head	Marconi Station	Coast Guard Beach	Duck Harbor
Ammophila breviligulata	10.2 ± 3.7 100	12.6 ± 5.8 100	37.4 ± 14.2 100	23.1 ± 11.0 100
Artemisia caudata	0 0	0 0	0 0	0.48 ± 1.3 13
A. caudata seedling	0 0	0 0	0 0	0.30 ± 1.2 8
A. stellariana	0 0	0 0	0.41 ± 1.8 5	0 0
Cakile edentula	0 0	0 0	1.9 ± 3.1 46	0 0
Carex sp.	0 0	1.1 ± 3.2 15	0 0	0 0
Lathyrus japonicus	0 0	0 0	0.51 ± 1.8 (0.18) 18	1.2 ± 2.6 25
Polygonella articulata	0.05 ± 0.32 3	0.05 ± 0.22 5	0.03 ± 0.16 3	0 0
Solidago sempervirens	0 0	3.2 ± 3.4 (0.67) 67	0 0	1.4 ± 4.2 40
S. sempervirens seedling	0 0	0.05 ± 0.22 5	0.13 ± 0.52 10	0.08 ± 0.35 5
Other species	0 0	0 0	0.10 ± 0.64 5	0.03 ± 0.16 3

total seedling emergence for Duck Harbor was 5.97 seedlings/ 1767 cm^3 and ranged from 0.05–0.34 seedlings/1767 cm^3 for the other three sites. For High Head, Coast Guard Beach, and the Marconi Station sites this is equivalent to approximately 3–20 seedlings/m^2 of surface area. Even this is a generous estimate based on the surface area collected by the cylindrical sampling device (15 cm diameter $\times$ 10 cm depth) and is based on the unrealistic assumption that all seeds to a depth of 10 cm are capable of germination. The paucity of seeds in the soil may be the result of poor seed production, intense pre- or post-dispersal seed predation (Louda 1989), pathogen attack, short seed lifespan, transport of seeds out of the dune habitat, or deep burial of seeds. However, little is known about the role of any of these factors in coastal sand dune communities (Ehrenfeld 1990; Maun 1985). Even less is understood about seed bank processes in backdune regions as most studies of sand dune seed ecology have focused on the foredune and strandline (Ehrenfeld 1990).

The predominant dispersal mode in sand dune species is wind (Ehrenfeld 1990) which is commonly associated with long-distance transport of seeds. Primary and secondary dispersal by wind can deposit seeds in favorable microsites or have the undesired effect of removing seeds from the system by dispersing them beyond suitable sand dune growing sites. Few studies have been conducted on seed dispersal in sand dune plants. Surprisingly, several studies of sand dune plant species have reported short-distance dispersal of seeds to locations close to parent plants (reviewed by Ehrenfeld 1990). Trapping of seeds by vegetation and settlement in depressions in the sand may influence the final resting places of wind-dispersed seeds. Such trapping effects can produce a clumped distribution of seeds in the seed bank and we have observed concentration of seeds in depressions soon after release from parent plants. However, this surface pattern becomes less obvious over time. We have also observed clusters of seedlings emerging from buried infructescences of *Ammophila breviligulata*, *Artemisia caudata*, and *Solidago sempervirens* and believe that burial of infructescences that have not released all their seeds may be an important determinant of clustering of seeds in the seed bank. These two processes most likely explain the highly clumped pattern suggested by our seed bank study.

There is a poor correlation between adult abundance and species representation in the sand dune seed bank. *Ammophila brev-*

Table 3. Relative abundance of all adult species found at each study site.

Species	Common name	Family	Abundance
High Head			
Ammophila breviligulata Fern.	Beach Grass	Poaceae	Dominant
Polygonella articulata (L.) Meissner	Jointweed	Polygonaceae	Frequent
Marconi Station			
Ammophila breviligulata Fern.	Beach Grass	Poaceae	Dominant
Artemisia stelleriana Besser	Dusty Miller	Asteraceae	Occasional
Carex sp.	Sedge	Cyperaceae	Rare
Chrysopsis falcata (Pursh) Elliott	Sickle-leaved Golden Aster	Asteraceae	Frequent
Cyperus polystachyos Rottb.	Sedge	Cyperaceae	Occasional
Euphorbia polygonifolia L.	Seaside Spurge	Euphorbiaceae	Frequent
Hudsonia tomentosa Nutt.	Beach Heather	Cistaceae	Occasional
Myrica pensylvanica Loisel.	Northern Bayberry	Myricaceae	Frequent
Oenothera fruticosa L.	Sundrops	Onagraceae	Rare
Polygonella articulata (L.) Meissner	Jointweed	Polygonaceae	Occasional
Rosa rugosa Thunb.	Rugosa Rose	Rosaceae	Occasional
Solidago sempervirens L.	Seaside Goldenrod	Asteraceae	Abundant
Coast Guard			
Ammophila breviligulata Fern.	Beach Grass	Poaceae	Dominant
Artemisia stelleriana Besser	Dusty Miller	Asteraceae	Abundant
Cakile edentula (Bigelow) Hook.	Sea Rocket	Brassicaceae	Abundant
Lathyrus japonicus Willd.	Beach Pea	Fabaceae	Abundant
Phragmites communis Trin.	Common Reed	Poaceae	Rare
Polygonella articulata (L.) Meissner	Jointweed	Polygonaceae	Frequent
Rhus radicans L.	Poison Ivy	Anacardiaceae	Occasional
Rosa rugosa Thunb.	Rugosa Rose	Rosaceae	Occasional
Solidago sempervirens L.	Seaside Goldenrod	Asteraceae	Abundant

Table 3. Continued.

Species	Common name	Family	Abundance
Duck Harbor			
Ammophila breviligulata Fern.	Beach Grass	Poaceae	Dominant
Artemisia caudata Michx.	Wormwood	Asteraceae	Abundant
Artemisia stelleriana Besser	Dusty Miller	Asteraceae	Frequent
Hudsonia tomentosa Nutt.	Beach Heather	Cistaceae	Rare
Juncus greenei Oakes & Tuckerm.	Rush	Juncaceae	Frequent
Lathyrus japonicus Willd.	Beach Pea	Fabaceae	Abundant
Lechea sp.	Pinweed	Cistaceae	Frequent
Polygonella articulata (L.) Meissner	Jointweed	Polygonaceae	Occasional
Prunus maritima Marshall	Beach Plum	Rosaceae	Rare
Rosa rugosa Thunb.	Rugosa Rose	Rosaceae	Occasional
Solidago sempervirens L.	Seaside Goldenrod	Asteraceae	Abundant

iligulata was the numerically dominant species at all sites and represents the most abundant indicator species on the sand dunes of eastern North America north of the Carolinas. *Solidago sempervirens* was the second most abundant species at all sites except High Head, which had been replanted with *A. breviligulata*. Despite being the dominant adults, these two species were present in very low densities in the seed bank (< 9 individuals/m^2). In comparison, the greatest seedling emergence was by *Artemisia caudata* (335/m^2) at Duck Harbor, where its adult density averages only 1.9/m^2. These results indicate that adult species abundance may not be a good predictor of species representation in the seed bank. This conclusion is not unique to sand dune communities and has been noted for many other communities, particularly in wetlands dominated by adults with clonal growth morphologies (Baldwin et al. 1996; Leck 1989; Shumway and Bertness 1992).

Emerging seedling densities, adult densities, and species richness were markedly lower at the most recently replanted site (High Head) than at the other three sites (Table 1). Nine, eleven, and twelve different species of adults were observed at Coast Guard Beach, Duck Harbor, and Marconi Station, respectively, while High Head supported only two species of adults (Table 3). The two replanted sites, High Head and Marconi Station, supported *Ammophila breviligulata* densities that were 2 to 3 times lower than at Coast Guard Beach and Duck Harbor (Table 2). Despite the lack of historical human disturbance, Coast Guard Beach and Duck Harbor are located closer to the foredune and, as a result, probably receive greater input of sand and nutrient deposition from sea spray, which may increase growth in *A. breviligulata*. The lowest overall seedling diversity and seedling number was at the High Head site, which was replanted in 1989, suggesting that heavily disturbed, unstable areas (marked by significant erosion) have depauperate seed banks. The highest seedling emergence was at Duck Harbor and can be attributed to a single species. When *Artemisia caudata* is removed from the data, Duck Harbor has similar adult plant abundance and diversity of species in the seed bank as the Marconi Station and Coast Guard Beach, which have been in a state of recovery for over 30 and 10 years, respectively. Similarly, the difference in the total number of seedlings emerging across all sites remains significant without *A. caudata* in the data set ($\chi^2 = 8.77$, $p < 0.05$). Marconi

Station, Coast Guard Beach, and Duck Harbor have significantly more seedling emergence than High Head.

All sand dune communities are subject to disturbances that result in movement of sand. Our initial intent was to compare the seed banks of sand dunes with histories of intense anthropogenic disturbance with "undisturbed" dunes that were not subject to anthropogenic disturbance. However, natural and anthropogenic disturbance may both have important consequences for sand dune seed banks. Increased aeolian sand transport enhanced by anthropogenic disturbance of sand stabilizing vegetation (High Head) may cause permanent removal of seeds carried with eroding sand. Natural overwash (Coast Guard) may also effectively remove seeds from the seed bank by burying them too deeply for germination to occur. Either process would result in a depauperate seed bank and would provide similar results in a study such as ours. A second goal of this study was to assess the potential for existing seed banks to restore species diversity to degraded dunes replanted with *Ammophila breviligulata* and the feasibility of using sand imported from other dunes for this purpose. The results indicate that sand dune seed banks have low species diversity and low seed densities and therefore are not likely to be useful additions for restoration efforts aimed at increasing sand dune species diversity.

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